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EVOLUTION.—*The mechanism of organic evolution.*¹ CHARLES B. DAVENPORT, Department of Genetics, Carnegie Institution of Washington. (Communicated by W. J. HUMPHREYS).

As we look over the world today we see, as the ancients did, the marvellous phenomenon of a world populated not only by humans but also by many hundred thousand so-called species of animals and plants existing in uncountable individuals whose number can no more be expressed by the ordinary system of numbering than astronomical distances can be readily expressed in miles. A cubic millimeter of the blood of a leucaemic mouse may contain over a million white corpuscles; and there may well be 1,000 such cubic millimeters of blood in a mouse. This gives us a billion white corpuscles in one mouse, not to consider the other cells of the mouse's body. These white corpuscles are essentially organisms, with powers of food-gathering, assimilation, excretion, locomotion, sensation, etc. And this is but one mouse. Even if we assume so few as $2\frac{1}{2}$ house mice to a human being on the earth (and mice are ubiquitous) we shall have 5 billion billion white blood corpuscles in house mice alone. But probably the pathologist might have as many bacteria in *one* of his test-tubes.

I have sometimes speculated on the number of organisms visible to the low power of the microscope that are in our Inner Harbor at the end of August, when it has a creamy, soup-like consistency. Assuming 1 per cubic millimeter, which is certainly far too small, there would be a quadrillion individuals in this space which would occupy only a square millimeter in the one-millionth map of the world, which has over half a billion square millimeters.

¹ Presented before the 233rd meeting of the Academy, as one of the series of papers on Origin and Evolution. Received for publication April 28, 1930.

Pardon me for wearying you with figures. I have wanted to put you in a position to grant my first point that the number of individual organisms on the globe is essentially infinite, though the number of kinds that naturalists have been able to count and describe in the past 150 years is still finite.

Next, I would call to your attention that most of these individuals have a short life and are quickly replaced by others, even if we leave out of account the unicellular organisms which retain their individuality only for the few hours or minutes necessary to reorganize and divide again. Even if we assume that the average length of life of an individual is a year—and it is probably not over a day—then we have to consider the remarkable phenomenon of an annual wiping off of the slate, as it were, of this infinitude of individuals each year and their re-formation the next year. This is possible owing to the immense reproductive capacity of certain species. Thus one oyster may lay 50,000,000 eggs during a few days in the summer and one sea urchin 20,000,000 eggs. These are samples, merely, of reproductive capacity of individuals. Perhaps now we have gained some conception of the number of individuals that have been produced each year on the earth, during we do not know how many millions of years.

If now you are willing to admit that the problem of organic evolution is that of the evolution of an organic mass consisting of an infinitude of individuals reproduced during an infinitude of generations, that may serve as a starting point to our inquiry as to the mechanism of organic evolution. Thank you!

Now, each individual has a certain recognizable form and acquires it through a certain course of development, be it more or less complex. The center of control of this form is largely, if not chiefly, in the chromosomes of the organic cells,—in its genes, to be more precise. In fact the soma of organisms, what we see, is just an index of the form-producing and maintaining factors of the genes—always, of course, recognizing that the end result is a sort of reaction between gene and environment. Now if the world of organisms is composed of an infinitude of kinds it is because the germ plasm is of an infinitude of kinds. The course of organic evolution has been, and is, what it is because the germ plasm has undergone and is undergoing the changes that it has undergone and is undergoing. This change of the germ plasm is called mutation. Mutation is one of the great factors in organic evolution.

Now what do we know about mutation? First, we know that it is wide-spread. This knowledge has first become precise, as organisms have been studied in successive generations, under controlled conditions.

Such mutations have long been known among domesticated organisms like potatoes, poultry, guinea pigs and dogs. Mutations have been so long known among domesticated organisms that it was natural for Darwin to discuss "Variation under Domestication" and for him and others to consider what quality of domestication it is that induces mutation. During the past 25 years in several species of animals taken from the wild, many generations have been followed. And in consequence we now know that mutation has not necessary relations to domestication; but only that domestication enables us to see and perhaps preserve such mutations. Rather, I should say, the product of such mutation, for the mutation has occurred in the germ plasm before it has become visible in the soma of the organism that develops under the control of the mutated germ plasm.

Let us now consider some of the facts of mutation that experimental study has revealed.

First, mutation is probably universally occurring in all germ plasms. Thus, in various mammals that have been reared so that they can be observed, mutation has occurred in all visible parts, in internal organs, and in resistance to disease. In man, which is the mammal that has been most thoroughly studied, we have mutations in hairiness, pigmentation, skin growths, appendages and digits, teeth, sense organs, form of internal organs, like the iliocecal valve, size and functioning of the endocrines, structure and functioning of the nervous system, of the blood and of the reproductive system. Finally, we have mutations in disease-resistance, due to obscurer morphological or bio-chemical idiosyncrasies.

Among pigeons, mutations in color, form of beak, nervous behavior have arisen in the Whitman-Riddle series. In poultry, I have in the course of 10 years got apparently new mutations in toes, wings and nervous reactions. And any poultry fancier knows of the mutations that have occurred in the past 75 years in color and pattern, in comb, in cerebral hernia and crest, in feet, wings and beak, and in egg-laying capacity.

In the insects which have been bred for rapidity of generations mutation has been repeatedly found. In *Drosophila*, Muller computes that among 500 factors in the X-chromosome of *Drosophila* each, in the average, mutates at the rate of 1 mutation in 4 years. This would seem to mean that, if you followed a single chromosome and when it divided considered one of the daughter chromosomes and so proceeded through the generations, then at the end of 4 years the

expectation is that in this line of chromosomes some one gene will have mutated and at the end of 4 more years that gene, or some other in the chromosome line we are following, will have mutated again. But there is an infinitude of chromosomes in the totality of all *Drosophila melanogasters*. The number in a single gonad is vast; the number of gonads in the world of Drosophilas that swarm in the autumn over every mass of decaying fruit in a million of orchards as elsewhere is practically infinite. One sees that just *Drosophila melanogaster* is producing an infinitude of mutations each season, and it has been producing this infinitude annually for a long time; but time does not count for much, for infinity times a finite number remains infinity. *Drosophila* throws upon the world each year, a vast number of kinds of mutations in inconceivably great numbers.

And *Drosophila* is not exceptional. Let us take a small water crustacean, one of the Daphnids. Banta has reared lines of these in captivity and examined the progeny daily. In one line of *Moina macrocopa*, carried parthenogenetically, a dominant mutation has occurred, on the average, at least once in 50 generations, but many more recessive mutations have occurred and been phaenotypically unexpressed. Now the number of Daphnids, which crowd any suitable pond in both hemispheres during each spring and autumn, is beyond conception. For a single circular pond a hundred feet in diameter may well contain, during the season many million Daphnids, if 1 is allowed to the cubic centimeter. The total of mutations that occur in one year in *Moina macrocopa* must be inconceivably great.

Certain of the lower forms are mutating even more strikingly. At least such would seem to be the case if the remarkable variations shown by Leonian in the fungus, *Fusarium*, may be regarded (as seems most probable) as mutations. Here scores of strains arise, in but a few years, even in a uniform culture medium, and perpetuate themselves. The strains vary in their rate of growth, pigment formation, type of fruiting, kind of spores, and reactions toward temperature, acids, dyes, and toxic substances. Apparently such mutation is going on all the time in nature.

As we consider these best known cases of mutation and realize that all of the countless chromosomes and genes are undergoing occasional change we are appalled by the universality of mutation and are caused to wonder how any species remains constant in nature to the extent that it is possible for a second naturalist, 50 years later, to identify in nature the species already described; we are less surprised that the

reviser of a genus a generation or two later will find twice as many species as his predecessor. We gain a lot of sympathy for the much abused species-splitter who, observing nature without the restriction of tradition, finds vastly more species than had been previously described by his predecessors. [Slides of variations in feral species (species-groups) were shown. These are probably cases of mutations that have established or may establish biotypes or incipient species.]

Organisms seem to be producing mutations at an inconceivably rapid rate, in infinite quantity. The wonder is that there are such things as species. One is led to inquire if, in describing species, taxonomists are not merely inventing transient, evanescent categories.

Such a conclusion is unjustified. Every taxonomist will tell you that the things he describes and others have described before him are real entities. If I am studying thrips and wish to secure a species described 50 years ago as living in a certain composite plant in eastern Russia, then if I go to the designated locality and look in the designated species of flower I will find the species with all the characters described 50 or 100 thrips generations ago. How is such an experience in constancy to be harmonized with universal mutation? This is perhaps the heart of the problem of evolution.

In considering the fixity of some species it must first of all be recognized that a species is a complex of morphological and physiological characters that can not exist alone but is absolutely dependent upon the external world for its existence. The organism must live in a medium of such and such physical qualities, at such a temperature, in the midst of such radiant energy, with access to such and such food stuffs which it is capable of taking in and utilizing for its metabolism. Every organism is extraordinarily closely fitted to its environment. And that environment may be very complex.

I will illustrate this principle by reference to the almost microscopic Collembola that live on the beach at Cold Spring Harbor (Fig. 1). They live in an area of apparently washed sand and pebbles in a region that is covered twice a day several feet deep by sea water and then exposed to the air, in a region swept by strong winds, overlaid by ice in winter, and exposed to the hot sun's rays in summer (Fig. 2). A region where the sandy substratum is caused to shift by the action of waves, and its pebbles to roll. The region looks unpropitious for any organism, yet of one species of Collembola in an area a kilometer long and 5 to 8 meters broad there are probably in the middle of summer a hundred million individuals. And they are meeting successfully the

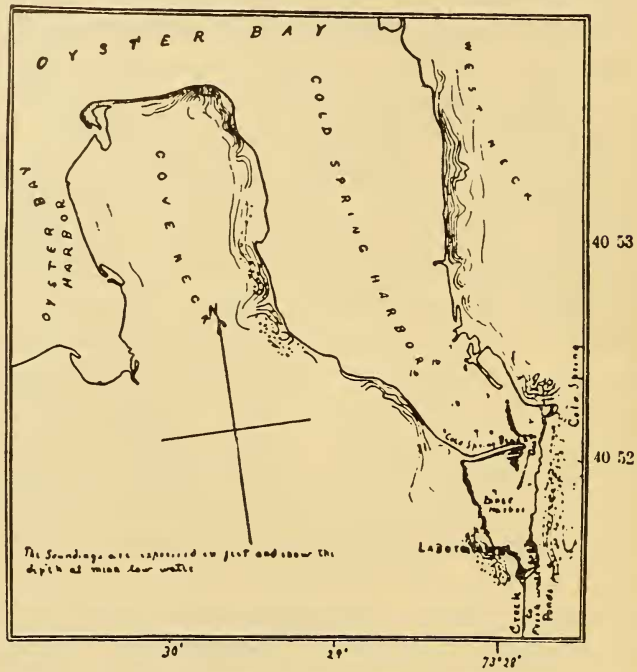


Fig. 1.—Map of Cold Spring Harbor, showing spit (Cold Spring Beach)



Fig. 2.—Photograph of north side of sand spit, near the western end, at low tide. In the central foreground is the high tide line, marked by a mass of debris. On the left is the gravelly lower beach; the middle beach and storm bluff are at the right.

difficult and complex conditions imposed by that particular habitat. If the habitat be compared to a most intricate lock, the organism is a most intricate key that fits that lock completely. How has this key come to fit this lock?

First of all, it is to be said that the Collembola in question is the only larger organism that is found in any huge numbers on and in the great portion of the beach. Worms there are that live in the sand of the beach; crustacea and insects there are that feed on the débris that

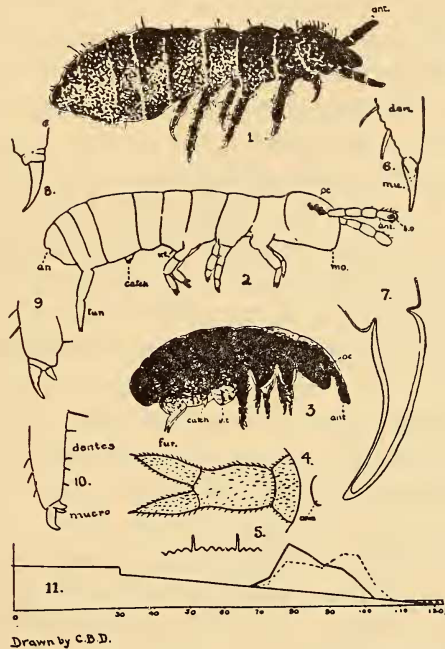


Fig. 3.—Drawings of 3 species of Collembola on the beach, (1), (2), and (3), with some details of their structure. (11) shows the relative frequency of *Isotoma* on the beach; the abscissae represent distances from the beach line on top of the beach; the ordinates, the proportional frequency of occurrence.

is thrown up by the sea at the high tide line; but it is only the Collembola that swarms over the beach (fig. 3).

Why are the Collembola the only organisms that make such use of the beach? The answer seems to be that they are the only group that holds a key approximating the needs of the beach lock. Two other species of Collembola live on the edge of the beach, in relatively small numbers. But one, *Isotoma berselsii*, has the combination of small size, slender form and greater capacity for jumping that are demanded for successful life on the beach. Another species which has a chunkier

form and is less successful as a jumper is found on the beach but is much less numerous than the first. Now the Podurid Collembola have, in general, a structure and reactions that lead them to live in situations not so very different from those occupied by *Isotoma*. They are found on water or in humid earth or in moist caves, or in crevices of moist walls. If anything is to survive in the sand of the sea beach it must come out of a group with instincts and structure that make it possible and preferable to live in such places. However, the interstices of the sand of the beach are especially fine and the period of exposure to the air is so brief that the insect must have movements and responsiveness of such sort as will ensure adequate exercise and oxygenation of the tissues during the brief time that it is exposed to the air. Collembola, in general, have the right form of key; *Isotoma berselsii* has precisely the appropriate notches to fit the precise lock of the beach.

I have dwelt at length on the Collembola of the beach because they may serve to illustrate the principle that mutations become the characters of species and play a part in evolution *provided* they meet some demand of the environment; or, the other way round, a new mutation persists as a species character if it can find an environment to which it is suited.

This general principle is of wide application. In Banta's daphnids there appeared a female whose young died on a cool day in the autumn. It was found that subsequent broods could be kept alive in an incubator at a higher temperature than that of the room. In short, an investigation of the temperature relations of these cold-sensitive young and their equally cold-sensitive descendants showed that there had arisen by mutation a thermal clone—a parthenogenetically reproducing strain—whose optimum temperature was about 10°C. higher than that of the ordinary daphnids. This mutation was fatal at the ordinary room temperature; it had important survival value for the environment of an incubator; it would have had an important evolutionary value had there been a warm spring near by into which the strain could have been transplanted. This experience, indeed, shows the probable method by which aquatic animals have come to inhabit hot springs. It is not by gradual change wrought on the germ plasm by the direct action of the high temperature of the water, but rather the fine opportunity for survival afforded by the high temperature to any chance thermal mutant.

Again, as has long been known, many of the animals that live in caves are blind and much speculation has been offered to account for this blindness. The old idea was that, through disuse and the parsi-

mony of nature that would prevent it from continuing to form useless organs, the useless organs were no longer formed. On the other hand, Eigenmann, through his extensive knowledge of fishes, was able to point out that the blind fish of caves belonged to just one family of fishes, a family that had mutated in the direction of blindness in various parts of the continent. Now, some of these mutations in the direction of blindness have survived even where there are no caves, but where there are waters running through densely wooded swamps and characterized by dark holes where poor sight is no handicap to the fish. When a blind mutation arose in that family of fishes living in the region of limestone caves of Indiana and Kentucky, that mutation was no handicap to its possessor. For the possessor had other sense organs sufficient to secure its prey. The waters of the cave, indeed, removed competition; and in other ways afforded an extraordinarily favorable environment for this genus of fish.

Another illustration may be afforded by still another group of animals. As you know there are vast numbers of molluscs living in the sea and in fresh waters; clams, oysters, periwinkles, cuttle fishes, squids are familiar marine molluscs. But there is a group of molluscs that has a history quite as striking as that of the cave fish. This group lives on the land, and sometimes, in very dry situations, even semi-deserts. In this situation the molluscs breathe by lungs instead of gills. How have the land molluscs—the pulmonates, including the snails and slugs—come to live on the land? One explanation that has been offered is that some marine ancestors gradually moved into streams and higher up into ponds which dry up periodically and there became gradually modified to breathe air. The matter is not quite so simple. The river mussels live in streams and ponds that occasionally go dry; they perish under these circumstances by the million; and yet they have never become adapted to land life—the appropriate mutations have never been afforded. Our land snails are the end result of a long series of mutations that have permitted life on the land. The first mutations in this direction occurred in certain marine snails with a gill chamber whose opening is so small that it can readily be closed to prevent the ingress or egress of water. Any mutation in this direction would enable its possessor to enter into the between-tides zone.

Actually, there live on our shores shore snails, belonging to the family of Littorinidae inhabiting a level where they are exposed to air for 12 to 20 hours of the day. Indeed, among the Littorinas one finds species that differ greatly in their emancipation from the sea. During

the recession of the tides the *Littorina* keeps the opening to its mantle chamber closed; so its gills are held in a medium of saturated air (fig. 4).

Now, it is out of this general group to which the *Littorinas* belong that the land snails have arisen. Any continued mutation in the direction of gill reduction or enclosure of the mantle cavity would have been in the direction that would have permitted the possessor to pass to dryer parts of the shore line and, incidentally, to escape from its enemies. The point is that not just any group of marine snails was able to adjust itself to land life, but only a group in which favorable mutations arose. The land crabs and the lung fishes represent the end stages of a similar evolutionary history to that of the land snails.

While it appears from these considerations probable that adjustment to extreme conditions of life has been rendered possible by favorable mutations, it still remains to consider what light modern genetical studies throw upon the details of this process.

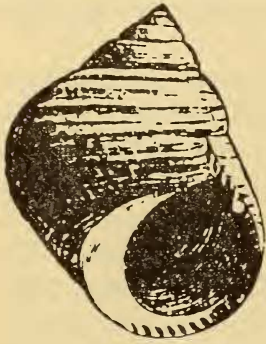


Fig. 4.—*Littorina litorea*.

We have seen that reproduction is unlimited and that mutation is constantly occurring; not to be sure in infinite amount in all directions equally but abundantly in certain genes; more rarely in others. We have now to consider in turn what induces mutations; what gives direction to mutations; how are the adaptations in nature brought about?

First, the causes of mutation are clearly determined, in part, by the unstable nature of the gene itself. The genes are very complex molecules, or rather groups of molecules. Now, many complex molecules are known in chemistry that are so labile that they break down almost spontaneously. How many compounds have to be kept in the dark, at a low temperature, undisturbed in order that they may "keep" at all. In time they "spoil", even under the best of conditions. The rate of change may be accelerated by heat, light and irradiation. The genes are not exceptions to the rule of change in labile substances. While the nature of the process of mutation in the genes has shown itself little influenced by external agents the velocity of spontaneous change is readily altered. Thus Muller, Hanson and others find the speed of mutation accelerated by increase of temperature, and by X-rays. No new mutations have been brought forth by the X-rays, but mutation occurs more rapidly. The X-rays do not direct evolution,

or even mutation, qualitatively, but afford opportunity for more rapid evolution by providing, in larger amount, one of the factors—mutation—necessary to evolution.

The fact that X-rays may accelerate the process of gene mutation has led some to the conclusion that all mutation is due to radiations. No doubt conditions compatible with the life of the soma *may* be found that will not permit of mutation, but it does not seem probable that this will ever be the case. Just the conditions essential to life probably provide the conditions for gene mutation.

Second, what gives direction to mutations? It is obvious that the organic world is far from being the infinitely diverse collection of haphazard and meaningless variants that we might expect were mutation entirely uncontrolled. It seems probable that, under ordinary conditions, genes break down or disintegrate in orderly fashion dependent on the nature of the gene. An illustration, which may be more than a mere illustration, is afforded in the rare earths where uranium breaks down into radium and radium into lead. Each stage, in turn, is determined by the immediately preceding stage.

So, in organisms, the mutations are usually of a recessive nature, which seems generally to imply that they are produced by a loss of something from the parental gene. In the different species of one genus the same kind of mutations occur. Thus between *Drosophila melanogaster*, *D. simulans* and *D. virilis* quite parallel mutations occur and are identified in many cases with genes occupying comparable loci in the chromosomes. Among mammals with which we are naturally best acquainted certain mutations occur again and again. Thus albinism, coat-color-pattern, hairlessness, elongated hair, reversed hair, taillessness, abnormal hands and feet, particularly digits, horns or hornlessness, achondroplasia. The recurrence of these mutations in various species of mammals, as tabulated by Osborn (1912), indicates that mutations are far from haphazard in origin, but probably depend upon the same genes with the same structure and capacity for change.

Finally, the mutations with which we are familiar constitute only a fraction of those that occur. Every student of intra-uterine stages of mammalian development is familiar with the phenomenon of intra-uterine deaths. So far as our observations go, it appears that in mammals more young die *in utero* than are born. Every student of development of sea urchins and other marine organisms knows that a large proportion of those that start to develop do not proceed far. We

see that early developmental stages are those in which great selection takes place; probably because the embryos carry non-viable mutations. From this point of view the individuals that reach maturity constitute the fraction that have undergone no *lethal* mutation.

The fact of lethal mutations (for they have been demonstrated in many cases) helps us to understand the other fact that in the midst of the world of mutations the organisms that come through are more or less well fitted to survive; they are not always the best, but they are good enough to pass the censorship of environment.

And this brings us to a consideration of the phenomenon which Darwin stressed, namely, of adaptation to environment. We have already seen that such adaptation is partly brought about through the selection by the organism of an *environment* that is adapted to it. We may now consider the case of selection by the environment of *organisms* that are adapted to it. In general, the organism must be able to play properly its part in the flow, in and out, of the chemical agents, water and food stuffs, upon which its life and activity depend. It must be capable of meeting emergencies of climate and organic enemies. It must pass the censor at every stage or be squelched.

A little experience of my own, on which I published some years ago, will serve to show how strict is this censor. I reared a large number of chickens to the one pound stage and had about 300 running over a grassy plot on about the tenth of May, at a time when crows are feeding their nestlings and hunting especially meat for them. About 40 per cent of the birds had a white plumage, 40 per cent a black (or nearly black) plumage and 20 per cent a plumage in pencilled, or striped markings, more or less like that of the ordinary game, or the jungle fowl. Of these the crows killed 24. Expectation, on the basis of random attack on the birds, was that about 9.6 would be white, 9.6 black and 5 pencilled. Actually there were killed ten white, thirteen black or prevalingly so, and one coarsely mottled gray and buff. No truly pencilled bird was killed. This observation tends to illustrate the principle that the self-colors in wild birds tend to be eliminated because conspicuous to their enemies; birds with mixed pattern are relatively immune from attack because relatively inconspicuous.

Now, though it has not been experimentally proven, yet the hypothesis may be entertained, that the presence of light colored mice in limestone regions and of dark colored mice on lava beds may result from an elimination of mutations that are in disharmony with the background. To nocturnal predaceous animals, like the owls which catch

mice, a white or light yellow mouse on a black lava bed would be seen and captured before a black one.

One further fact must be taken into account in considering the adjustment of organisms to their environment, and that is that change of environment may well cause, and apparently has in the past often caused, the elimination of species over the whole extent of their area of destruction.

Consider how wide-spread must have been the consequences on the fauna of the northern hemisphere as far south as Long Island and even further south of the great ice sheets that covered the circumpolar territory in glacial epochs. Many poorly clad species of mammals must have found the icy conditions insupportable; just as the mastodon and mammoth did. The change in environment may be of a more subtle sort. Thus the great size and herd instincts of the bison enabled it to develop enormously on the extensive plains of North America and rendered it more than a match for the Amerinds living in a stone age. Just this size and number wholly unfitted these mammals for the new environment of the aggressive, agriculturally inclined white man, armed with a rifle. Agriculture and free-ranging bisons could not coexist and the rifle eliminated the mammals. So today the great size and aggressiveness of the large mammals of Africa are a challenge to the sportsman and the future seems to spell extinction for them. Here we have to do with elimination resulting from what may be called a cultural evolutionary "mutation"—the rifle.

But man's part in evolution is not merely in the elimination of his large enemies, which he has all too thoroughly mastered, but in his struggle with the small and innumerable insects that threaten his agriculture as it becomes more intense. The more successful and prolific an insect injurious to agriculture is the more certainly will it arouse man's destructive energies and the greater the certainty that the all too favorable mutation that is the cause of its success will be the cause of its elimination in whole, or part.

But mutations of a still more dangerous sort are threatening mankind—mutations in the world of organisms that live as parasites on the human protoplasm. With the more conspicuous of these parasites, external and internal, man has learned to cope. One by one the pathogenic bacterial diseases are being eliminated or reduced in frequency. But now we face still smaller parasitic particles—the filterable viruses—which are, at present, practically inaccessible to man. There seems to be reason to conclude that they are mutating, also, and